CULTURAL STUDIES ON THE GENUS GREVILLEA IN HAWAII

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"A shrub, or a trailer, or maybe a tree,
With flowers massed together, Grevilleas are we.
We haven't got all of the usual flower "things";
We each have two seeds, though they seldom have wings.
We're sometimes called 'spiders'--so, as you can see,
We're flowers that are different as can be."

A Child's Poem (71)

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I. INTRODUCTION

The Proteaceae family contains 62 genera, 37 of which are native to Australia, while the other 25 genera are distributed in Asia and the southern hemisphere, most notably South Africa (20). The South African group contain the genera Protea, Leucadendron and Leucospermum while the Australian group include such genera as Banksia, Grevillea, and Hakea; all of which have been introduced to Hawaii as potential horticultural crops.

Eighty percent of Australia is arid or semi-arid, and most of the Proteaceae evolved within 50-150 miles of the eastern, southwestern, or southern coasts under climates characterized by long, hot summers and mild winters (Appendix Table A). The Proteaceae dominate the scrub (0-8 meters) and heathlands (0-2 meters), the soils of which are composed of shallow or deep sands, sandy loams, or lateritic gravels (45, 66). These soils are some of the most infertile in Australia, containing low levels of nitrogen, phosphorous, and trace elements (9, 10, 11, 45, 95, 96, 97). Many proteaceous species have adapted to the low availability of the mineral elements and addition of even moderate amounts of fertilizers, particularly phosphorus, may be toxic to these plants (9, 11, 42, 45, 53, 55, 64, 95). Most of the members of this family do best in full sunlight, but will tolerate filtered light (66).

The adverse environmental conditions under which the Australian Proteaceae evolved, such as hot, dry summers; infertile soils with poor water-holding capacity; and frequent fires and droughts, have led to a

number of specialized features characteristic of the Australian Proteaceace. These adaptations include proteoid roots; mechanisms to direct high levels of nutrients to the seeds; lignotubers; woody fruits; leathery leaves with well-developed cuticles and sclereids; low water and mineral use; and the ability to start or stop growth at any time during the year, depending on whether or not the environmental conditions are right (9, 10, 11, 51, 52, 54, 55, 56, 62, 64, 65, 66, 67, 68, 89)

Even though the Proteaceae of Australia evolved under environmental conditions detrimental to most plants, this does not mean they will not adapt, or perhaps grow better, in other areas. For example, Grevillea robusta, native to the moist forestland of Queensland, has reached weed proportions in some areas of Hawaii and California, and Hakea suaveolens, which occurs in a narrow strip of coast in Southwestern Australia, became a pest when introduced to South Africa (66). Some Australian proteaceous species will adapt quite readily to a wide range of environmental conditions, while others may be restricted to certain habitats (66, 77).

In a preliminary field trial conducted in 1981, 18 Grevillea species of hybrids were planted at five locations in Hawaii to evaluate their growth under various environmental conditions (Appendix Table B). The localities differed in elevation, rainfall, pH, temperature, and soil characteristics. Many of the Grevillea survived only at some of the locations (Appendix Table C) and not at others. Although all of the environmental factors could have partially been responsible for the differing survival rates in the field plots, not all the environmental factors nor all of the grevilleas could be examined within the scope of

this study. One factor, soil pH, was chosen because one of the plants, G. glabrata, did well at locations with a pH range of 6.3 to 8.0 but did not survive at the more acidic locations of Manoa, Nuuanu and Wahiawa. Other grevilleas, such as G. gaudichaudii and G. 'Boongala Spineball', survived in all locations but the alkaline Kualoa location. The ease of propagating the material needed to establish this study was also a factor in determining which species of Grevillea would be used to examine the pH range that best growth could be obtained and to possibly relate the results of the field trial to the pH of the soil. Two Grevillea species, G. glabrata and G. biternata, were chosen to examine the relationship, if any, to the survival rates resulting from the field trial and the pH of the soil.

An extensive literature search indicated that little is known on the form of nitrogen associated with optimum growth in grevilleas, and a study was undertaken to determine the effects of different nitrogen sources on the growth of G. rosmarinifolia, since this species had been used in other nutritional studies (80, 102, 103).

A preliminary propagation study in which five commercial rooting preparations were evaluated on 15 Grevillea species or hybrids, resulted in poor or no rooting at all for three of the hybrids, regardless of the kind or concentration of rooting preparation used (Appendix Table D). The objective of the second propagation study was to examine the rooting ability of G. 'Ivanhoe', G. 'Poorinda Peter', and G. x hookeriana, when using two-node shoot sections, starting from the tip and including one section of mature hardwood, to determine if there was a gradient in rooting response along the stem.

II. LITERATURE REVIEW

Distribution and Plant Characteristics

The genus Grevillea is distributed from Australia (250 species) to New Guinea and New Caledonia (1 endemic species each), while none are found in New Zealand (20, 99). Fifty species occur in New South Wales, 35 species in Victoria, 40 species in Queensland, 1 species in Tasmania, with most of the remaining 120 or so species occurring in the Southwestern Province (74). In general, the genus is confined to sclerophyll forests and heaths, with only a few species occurring in the deserts or rainforests. Some 150 of the known 250 Grevillea species have been cultivated. Some adapt readily to a wide range of growing conditions while others are restricted to specific localities (53, 74). Molyneux (74) states that of the Western Australian grevilleas, those that evolved in the deep sands are difficult to establish, whereas those that evolved in shallow sands will adapt to shallow or deep soils.

A description of a number of Grevillea species and hybrids, and their use in the Australian landscape industry can be found in Appendix Table E. The growth habits range from 4-5 meter shrubs used as espalier, specimen, or hedge plants to prostrate shrubs used as rockery plants or groundcovers (31, 99). The genus is characterized by bilaterally symmetrical tubular racemes, sepals lacking, bracts deciduous at flowering, which are specially adapted to pollenation by higher insects, birds, and mammals (20, 54, 75). The inflorescence range in size from large "toothbrush" types to small clusters of waxy flowers. Flower color varies from white to pink, orange, red, and

two-toned combinations in some hybrids. Flowering usually occurs in the winter months in Australia (July-October) but some, such as G. bipinnatifida and G. chrysophaea, flower all year long (17, 31, 53). A number of the grevilleas in test plots in Hawaii flowered from December through May, with sporadic year-round flowering in G. 'Boongala Spineball' and G. gaudichaudii. The fruit is a follicle which opens when the seed is mature, releasing 2 seeds.

The most notable difference among the grevilleas is in the foliage characteristics (Appendix Table E). Molyneux (74) cites some examples of this: "In Queensland, a large percentage of species have a large pinnate, fern-like leaf, with most plants being large shrubs or small trees. In New South Wales there appears a dominance of simple leaves, either linear, obovate or lanceolate type leaves. In Victoria we have a large number with holly-like leaves. In South Australia they again have simple leaves in most cases, while in Western Australia you find a complete range, including simple leaves and holly-type leaves, but the very narrow divaricate type of leaf is quite common.

Culture

Although the majority of the grevilleas are adaptable and hardy, growth stops and the plant may die if the soil conditions and drainage are not right. Most of the grevilleas listed in Appendix Table E require full sunlight, good drainage and protection from strong winds (19, 99). A number of Australian nurserymen group the grevilleas in their sales catalogs by the growing conditions required for optimum growth.

In general, grevilleas do well on well-drained loam or sandy loam with a slightly acid to neutral pH, although some of the Western Australian natives are found growing in neutral to slightly alkaline soils (31, 53, 76). Grevilleas will also grow satisfactorily in soils containing clay if the soil is well-drained. Poor drainage often causes the death of the plant from poor aeration and Phytophthera cinnamomi (31, 74, 102).

Since the Australian Proteaceae evolved on very infertile soils, the moderate to high fertilizer levels applied to most foilage plants may be toxic to grevilleas (1, 66, 102, 103). It has been found in nursery trials that G. rosmarinifolia developed chlorotic foilage with full strength fertilizers and the plants were smaller when compared to plants grown with half-strength fertilizer or no fertilizer at all (102).

Most Australian Proteaceae are extremely sensitive to phosphorus (78, 79, 80), and Grevillea is no exception. Phosphorus toxicity has been described in grevilleas growing in soil-less potting mixtures and all but very low levels (less than 40 g/m^3) (81) are damaging and perhaps toxic (42, 78, 79, 80, 81, 102, 103). Symptoms of phosphorus toxicity, which appear at medium to high levels of phosphorus, include loss of leaf sheen followed by necrosis and abscission of the leaf and are exaggerated by high levels of nitrogen (42, 78, 102). Masses of proteoid roots are present when phosphorus is lacking and nitrogen is at a moderate level in the medium (42, 80, 103). Grevilleas differ in their susceptibility to phosphorus toxicity, and Australian researchers recommend 3.0 kg m^3 of Osmocote 18-4.8-8.3 or 18-2.6-8.3 for those

grevilleas tolerant of slightly higher phosphorous levels (.08 to .15 kg P/m^3), such as G. rosmarinifolia, G. arenaria, and G. thelemannia, and 2.25 kg/m^3 of Osmocote 18-2.6-10 (0.06% P) for the more sensitive G. 'Poorinda Firebird', G. aquifolium, and G. glabella (1, 78, 79, 81). Lime should be incorporated into a peat-based medium at the rate of 3.0 kg/m^3 (1, 19). Most grevilleas prefer a slightly acidic pH and the excessive addition of calcium to soils has been found to be toxic to a number of species (102, 103).

A number of grevilleas are said to adapt readily to container growing. G. hookeriana, G. barklyana, G. asplenifolia, G. caleyi, and G. ericifolia all make attractive patio or lanai specimens (99).

Most grevilleas produce flowers on new growth and benefit from annual pruning a few months prior to or after flowering (17, 31). Pruning increases the density of the plant and flower production.

Although grevilleas are relatively pest-free, many Australian nurserymen spray pesticides on a monthly basis for mites and leaf spot, Verucisporum proteacarum (19, 99). In addition to Phythophthera cinnamomi, P. parasitica has been reported on grevilleas when they are grown under acidic conditions. A number of growers have found that increasing the pH of the media seemed to inhibit the disease (70).

Propagation

The major factors which promote the root forming processes are optimum supplies of auxins, carbohydrates, and rooting cofactors, in conjunction with the physiological age of the stock plant and the environmental conditions under which the cuttings were taken. Indoleacetic acid (IAA) is the major naturally occurring auxin and

is synthesized in young leaves and other meristematic areas of the plant from where it moves basipetally down the stem. Its distribution in the plant is influenced by light and gravity and travels in the phloem parenchyma, cortex, or pith of the plant. Small amounts of IAA cause large responses such as renewing vascular activity, cell elongation, cell wall loosening, and the stimulation of RNA synthesis (12, 39). Indolebutyric acid (IBA) and naphaleneacetic acid (NAA) are synthetic compounds that cause many of the same physiological processes as IAA, and may be even more effective than IAA in many responses (12, 39).

Auxins act in the dedifferentiation of wounded stem cells and determine the sites of root initiation (39). IAA, or its exogenously applied synthetic counterparts IBA or NAA, may then combine with one or more rooting cofactors, and this complex then induces adventitious root formation (39, 40, 57). Rooting cofactors are endogenous substances which act synergistically with the auxins in the process of root formation (48). A number of researchers have found that cultivars of easy-to-root species have a higher endogenous content of cofactors in the stem than a difficult-to-root cultivar of the species (39, 48, 82, 83, 100, 101). Hess (48) and Girouard (40) have partially identified the components of four cofactor complexes as phenolic or oxygenated terpenoid compounds. The cofactors are hypothesized to be involved in the lignification of cell walls and account in part for secondary wall thickening (40).

Since the presence of leaves on stem cuttings has been found to enhance adventitious root formation, it has been assumed that this

is in part due to the carbohydrate production occurring in the leaves. Carbohydrates and the auxin-cofactor complex are required for root formation (18). Many researchers have found that exogenously supplied sugars and nitrogen compounds (such as KNO_3) in the propagating medium stimulated root formation in a number of difficult-to-root plants (13, 18, 86). Easy-to-root cultivars frequently have as much as 3 to 4 times more total carbohydrates in the stem than difficult-to-root cultivars (41, 100, 101), and Breen (18) found that in plum cuttings, the case of the cutting had accumulated 4 times as much labelled 14C sucrose when compared to the rest of the stem section.

Seasonal rooting is defined as the ability or inability of a plant to regenerate roots from stem cuttings at certain times of the year. Environmental factors such as temperature and light influence the amount of auxins, photosynthates and other growth stimulants required by the plant for the formation of adventitous roots (2). In general, propagative material taken from stock plants grown under high light and temperature, such as in late spring or summer, will have higher contents of auxins and carbohydrates when compared to material taken in the fall and winter (44). However, once the stem cuttings are placed in propagative beds, light may have an inhibitory effect by preventing root initial development (58). Temperature of the propagative medium may need to be maintained at 21^{o}-29^{o}C in many cooler areas by the use of heating cables (33, 63, 86). High relative humidity in the propagation area is required to prevent the dessication of the leaves and stem by lowering the transpiration rate. Intermittent mist systems have been an essential component of the nursery industry for many years.

Structural barriers of the stem (12, 86), inhibitors (48), and the improper choice of propagation media may also prevent root formation (44). The role of growth regulators and their effect on root formation has been investigated in the last few years (14, 25, 26, 59, 86, 111).

The vegetative propagation of a number of the Proteaceace has been researched recently in South Africa, Australia, and Hawaii (19, 25, 26, 32, 33, 34, 36, 37, 38, 63, 70, 84, 111). Many of the proteaceous species which are grown in these areas are highly valued for their use in the cut flower and foliage industry, and as landscape material. While some genera are difficult to root (25, 26, 84, 111), many of the grevilleas rooted easily as herbaceous or semi-hardwood cuttings when treated with IBA (19, 33, 37, 63, 70, 99). Most grevilleas are propagated by cuttings, and a few are produced either by seed, tissue culture, grafting, or air layerage (19, 33).

Since the follicle in which the seeds of grevilleas are produced releases the seed upon reaching maturity, the influorescence must be covered with a paper bag to collect the seed. The seeds are dormant when released and require a preplant soak and/or cold storage before they will germinate. Heselhurst (47) obtained a maximum germination rate of 70% for G. banksii using a .2% KNO_3 as a soaking treatment for 12-24 hours, and a potential of 90% germination if the temperature of the medium was maintained at 25-33^{o}C. Alternatively, Dupee and Clemens (33) found that the highest germination rate for G. banksii could be obtained if the seed coat was partially removed and the seed then stored at 12^{o}C for 2 months. The medium suitable for seed

propagation is either vermiculite or a mixture of sand and peat with the seed planted at a depth of 3-4 cm (33, 47).

A few Australian nurserymen use grafting to produce new, interesting horticultural specimens or as a means of propagating difficult-to-root species such as G. johnsonii, which readily grafts onto G. robusta seedlings (32, 34). Some grafts within the genus are very compatible while others are not. One-year-old G. robusta seedlings have frequently been used as the rootstock in the industry, and semi-hardwood scions of G. leucopteris, G. bipinnatifida, and G. gaudichaudii have been very compatible, while G. 'Robyn Gordon' and G. johnsonii moderately so (33). G. vestita, when used as a rootstock, has given an average success rate of 63% with G. bipinnatifida, G. johnsonii, and G. leucopteris scions (33). G. 'White Wings' and G. 'Ivanhoe' averaged 75% success with the scion G. bipinnatifida while G. lavendulacea has proven unsuccessful as a rootstock for any of the previously mentioned scions (33). Cleft grafting has given better results than chip budding, side grafting, or the whip and tongue graft (33).

The success of air layerage depends on the Grevillea used and the time of year the procedure is done. Air layers of G. robusta and G. banksii rooted 100% in the autumn, whereas the success rate in the winter was only 44% for G. banksii (33). Only 28% of the air layers of G. 'Robyn Gordon' rooted, while G. johnsonii air layers formed no roots at all in 12 weeks (33).

Vegetative propagation by stem cuttings is the most frequently used form of propagating this genus. Stock plants are generally replanted every three years, pruned back every four months to 1/3-1/2

their size, and flower buds are removed as early as possible all year long (19). Cuttings are taken in the spring just prior to flowering or after flowering has ceased at the end of the summer (19, 70). The medium used for stem cuttings is usually a 1:1 (v/v) sand:peat mix (33), with 3 kg lime/m^3 (1) or 1 kg dolomite/m^3 (19) added. There is wide variation in the amount of shade used; both 30% and 80% have proven satisfactory (33, 70).

Before the commerical availability of the quick-dip hormone solutions, Seradix 2 (3000 ppm IBA in talc) was the most commonly used hormone for rooting grevilleas. Ellyard (37) found that this preparation gave the same rooting percentage (86%) as a 500 ppm quick-dip containing IBA for propagation of G. baueri. Most Australian nurserymen at this time use a quick-dip containing IBA but the concentration varies with the Grevillea species, hybrid, or cultivar (33, 36, 37). In general, tip or semi-hardwood cuttings are treated with 1000-2000 ppm IBA. A few grevilleas such as G. laurifolia respond better to 500 ppm IBA while G. willisii requires 4000 ppm IBA, a concentration that causes a delayed burning reaction in most other grevilleas (19, 33, 36, 37, 70). Some grevilleas are sensitive to the inclusion of NAA in a quick-dip solution, either by itself or in any combination with IBA, and poor rooting percentages may result (37).

Nutritional Studies

pH

It has been known for many years that the pH of soil solutions can have a profound effect on the adaptability of a plant to a given soil and on the availability and absorption of the mineral elements

in that soil. In itself, an acid or alkaline soil reaction does not necessarily result in a serious impairment of growth but pH is interrelated to the plant species involved; soil characteristics such as the mineral and organic matter content; climatic factors such as precipitation, wind and temperature; and the previous usage of the soil (5, 6, 109). In general, the pH of a soil serves as an indicator of the interrelations between plant nutrients and the availability of these nutrients to the plant (6).

Plant species differ in their ability to absorb ions in different soil reactions and frequently plant growth results in a positive response only to a specific range of pH, while other plants have a wide range of pH at which they will grow. Arnon et al. (6) found that in the pH range of 3.0-9.0, bermuda grass would tolerate almost the entire range (not pH 3), while lettuce and tomato growth was severely restricted at pH 3, 4, and 9.

It is commonly accepted that the pH of a soil may have direct or indirect effects on the absorption mechanisms of the root, although it is difficult to distinguish between these effects and the effects of other soil factors (43, 46, 90). Direct effects usually result in an irreversible injury to the function and structure of cells in the root and the plant may die (90). Indirect effects of pH such as competition and solubility problems are the most frequently seen causes of growth reduction involving pH, and are usually reversible. In acidic soil solutions, many cations complete with hydrogen ions for absorption and the uptake of such cations as Ca, Mg, K, Cu, and Zn may be severely limited and deficiencies result. High concentrations

of hydroxide or bicarbonate ions in a soil solution result in competition for uptake and anions such as phosphate and nitrate may become deficient in the plant (43).

Nitrogen

Nitrogen is required by plants in the greatest amounts when compared to other nutrients and it is the element most likely to be deficient in most plants (72). Nitrogen is very mobile in the plant and contributes to the vegetative and reproductive growth, carbohydrate utilization, and is a component of amino acids, amides, alkaloids, and chlorophyll (21). Nitrate and ammonium ions are the most important sources of nitrogen utilized by plants, and the nitrogen source used in fertilization of crop plants can promote or adversely alter the growth and chemical composition of that plant (61).

Plants can utilize nitrate, ammonia, or urea and the better growth obtained when one nitrogen source or another is used in nutrient solution cultures is dependent on the concentration and availability of the ions in the solution, the pH of the growing medium, light intensities, temperature, and the specific plant (7, 21, 22). In the absence of soil and the nitrifying bacteria it contains, nitrogen is taken up in the form it is supplied (3, 4). Most plant species differ in the rate of assimilation of a particular nitrogen form and the form in which it is translocated to the shoots (7, 73). The assimilation of nitrate ions occurs in conjunction with the release of hydroxide or bicarbonate ions from the roots which increases the alkalinity of the growing medium (3, 4, 104). Once inside the plant, nitrate must be reduced before it combines with carbohydrate skeletons to form

amino acids (21). Under high nitrate fertilization, low light intensities, and low temperatures, stored nitrate, is not readily converted to ammonia and excessive amounts may be toxic to the plant and grazing mammals who may consume it (21, 72, 73). Ammonia can be absorbed by roots as NH_4, NH_4OH, or NH_3, which leads to the release of hydrogen ions in the approximate amounts of the ammonia taken up (3, 21). The ammonium ion, which usually does not accumulate in the plant, is readily available for conversion into organic nitrogen compounds and it is in this form that it is translocated to the shoots (21, 110). Accumulation of free-ammonia can occur and may be toxic to the plant if the assimilation in the plant is limited by the lack of carbon skeletons (110). Assimilation of the urea molecule is thought to be induced by the enzyme urease, which splits the molecule into NH_3 and CO_2, from where it is further converted to organic nitrogen compounds and translocated to the shoots (60). Since urea is taken up as a molecule, there is no release of cations or anions from the roots and the pH of the medium remains stable (60).

Extensive research over many years has determined what nitrogen source many crop and ornamental plants do best with. There is ample evidence that many plants can absorb and utilize ammonia without pH control (98, 104, 107), but even when the pH of the media is controlled, ammonia still limits the growth of some plants and may cause severe injury to others (3, 4, 61, 72, 87, 93, 110). Ammonia fertilization results in lower tissue concentration of cations such as Ca, Mg, K, and Mn, higher concentrations of P, Fe, total N, amides, organic acids, lower tissue pH and a reduction in water use efficiency (60, 61, 107,

110). Symptoms of ammonia toxicity vary with the plant but generally include reduced growth rates, wilting, marginal necrosis, and interveinal chlorosis of terminal leaves and it may eventually kill the plant (14, 22). The roots are usually darkened, small, and nonvigorous (7).

Most plants in nutrient solution cultures do best with nitrate compared to ammonium nutrition (4, 15, 23, 29, 30, 69, 72, 87, 88). Nitrate fertilization increases the uptake and tissue concentration of cations (7), decreases the uptake of inorganic anions such as PO_4 and SO_4, and increases the respiratory rate of the roots (23).

Urea usually gives an intermediate growth response when compared to nitrate and ammonium fertilization (30, 60) although some plants, such as pine, show increased growth when it is used over the other two (85, 108).

Ammonium nitrate gives intermediate growth responses when compared to nitrate and ammonia (88). Some plants can utilize ammonium nitrate with no harmful effects, and a few, such as peace, actually grow best with the combination (28, 35, 85, 102, 108).

III. MATERIALS AND METHODS

Propagation

A preliminatry investigation into the vegetative propagation of 13 Grevillea species or hybrids (Appendix Table D) led to another study. Three hybrids, G. x hookeriana, G. 'Ivanhoe', and G. 'Poorinda Peter', which had poor or no rooting response at 0 to 8000 ppm IBA. This experiment was conducted to determine if there was a gradient in rooting response from the tip to the base of a shoot.

The plant material was obtained from the Maui Agricultural Research Station at Kula, on June 21, 1983. The experiment was conducted at the Magoon Research Facility, University of Hawaii at Manoa, under 30% polypropylene shadecloth. The temperature ranged from 21-32^{o}C (106). The propagative material was stored overnight in a 15^{o}C cooling unit and was dipped in a fungicide solution (Dithane M-45 at 2 T/gal.) prior to making the cuttings the following day.

Two-node cuttings were made starting with the terminal cutting, containing 2 fully mature leaves, and progressing down the stem to include on section of mature hardwood. This resulted in 4 cuttings of each except for G. 'Ivanhoe', which had 5 sections due to the greater length of semi-hardwood. A quick-dip hormone solution was freshly prepared by dissolving .2 g IBA in 100 ml of a 50% ethanol-water solution, the resulting solution containing 2000 ppm IBA (36, 37). The basal portion of each cutting was dipped into the hormone solution for 5 seconds and the excess was allowed to evaporate before the

cuttings were inserted into a 1:1 (v/v peat:perlite mixture). The metal propagating trays were placed under intermittent mist (on 2 seconds/ minute). The experiment was established in a randomized complete block design with 5 replications and 10 cuttings of each section (treatment) per replication for each Grevillea hybrid.

Parameters used to measure rooting included: the dry weight (grams) of the roots per cutting, the percent rooting of each section, and the time required for the first appearance of roots. Evaluations for the first appearance of roots were made at weekly intervals by carefully lifting each cutting from the medium and recording the presence or absence of roots. If a root greater than 1 cm was observed, this was noted and the cutting was not removed from the medium again until the termination of the experiment.

The experiment was terminated after 8 weeks, at which time the cuttings were removed and washed free of media. The top portion of the plant was cut off at the media level, and the roots were dried at $60^{o}C$ for 4 days and weighed. Analysis of variance using, the arcsine transformation for the percent rooting, with mean separation by the Duncan/Waller multiple range test at the 5% level was performed using SAS (91, 92). Comparisons were made only within, no between hybrids.

Nutrition Studies

General Set-up

These experiments were conducted at the Magoon Research Facility under 30% polypropylene shadecloth. A clear plastic cover was erected five feet over the experimental areas to prevent the frequent Manoa

rains from leaching the treatment solutions after they were applied. Temperatures ranged from 18-29^{o}C in the winter and 21-32^{o}C in the summer (106).

Semi-hardwood cuttings of G. glabrata, G. biternata and G. rosmarinifolia were supplied by the Maui Agricultural Research station at Kula, were rooted under intermittent mist (on 2 seconds/minute). Uniform cuttings were established in 15 cm plastic pots in acid washed silica sand prior to applications of the treatments. Until the start of each respective experiment, all plants were established using a 1/4 strength Hoagland solution. All plants were watered every other day with 200 ml of the nutrient solution and the medium was rinsed with 400 ml of deionized water on the days they did not receive the nutrient solution. Iron (NaETDA) was supplied foliarly as a .5% spray once a week (49).

Parameters used to measure treatment effects included the dry weights of the roots and shoots, length of extension growth (the new growth increment of 3 lateral branches) and tissue analysis. The number of proteoid roots was recorded in the pH experiment.

The roots were washed free of sand at the end of each experiment and the data parameters measured. The foliar material used in the tissue analysis was dried in a 60^{o}C oven and ground in a Wiley mill (20 mesh screen). Tissue analysis was done by the University of Hawaii's X-Ray Quantometer Lab, model #7300. Analysis for total nitrogen was determined by the same lab using the Berthelot Method.

Analysis of variance with mean separation by the Waller/Duncan multiple range test at the 5% level was performed on all the growth parameters measured using SAS (91, 92).

pH

Results of preliminary field trials to evaluate a number of Grevillea species and hybrids under various environmental conditions in Hawaii suggested that soil pH may limit where they can be grown (Appendix Tables B and C). This study was to establish the pH limits within which healthy growth could be obtained for two Grevillea species (G. glabrata and G. biternata) used in the field trials. In the field trial, these two species performed best at different pH conditions.

The experiment was arranged in a randomized complete block for each species, with one plant per replication. The G. biternata set-up contained 8 replications and there were 10 replications of G. glabrata due to greater availability of plant material. Five pH treatments, 4, 5, 6, 7, and 8 were applied, using one plant per treatment per replication. A quarter-strength Hoagland #1 solution (49), which contained 56 ppm N, 7.5 ppm P, 25 ppm K, 40 ppm Ca, 9 ppm Mg, 16 ppm S, and a quarter-strength Hoagland micronutrient solution, were mixed in 5, 10 liter buckets. The pH of this stock solution was adjusted to the five treatments using .1 M KOH. The total K in each treatment was 25 ppm, and 10 ppm of this was contained in the stock solution. The original pH of the stock solution was 4.3, and the following amount of .1 M KOH was added to raise the pH, while .1 M KCl was added to balance the amount of K in each treatment solution:

pH	.1M KOH	.1M KCl
4	0	15 ppm
5	.75 ppm	14.2 ppm
6	2.75 ppm	12.2 ppm
7	8.5 ppm	6.5 ppm
8	15 ppm	0 ppm

The solutions were applied to each particular pot every other day, with each pot receiving 200 ml/day. Between each watering with a treatment solution, the medium was leached with 400 ml of deionized water to avoid any salt build-up. The pH of the solutions was measured with an Orion Research Digital Analyzer, Model 701/A, and the solutions usually varied .05-.10. Leachates from each treatment were caught weekly and measured with the pH meter. All leachates varied .1-.3 from the original treatment solutions (43).

The experiment was terminated on May 5, 1984, when many of the plants of G. glabrata in one treatment looked very poor. The three most recently matured leaves were taken from 5 shoots of each plant for tissue analysis. Regression analysis was performed on the tissue analysis results.

Nitrogen-source

The objective of this study, consisting of four nitrogen-source treatments, was to obtain more information on the effect of nitrate,

ammonia, urea, and ammonium nitrate when each was used as the sole source of nitrogen.

On January 7, 1984, 40 of the most unform plants of G. rosmarinifolia were selected, and this group of plants was then divided into groups of 10. The experiment was established in a randomized complete block design with 4 nitrogen treatments and 10 replications, 1 plant per treatment. Nitrate was supplied as $Ca(NO_3)_2$ (15% N), ammonia as $(NH_4)SO_4$ (20% N), urea (46% N), and ammonium nitrate (33% N). The four nutrient solutions differed chiefly in the form of nitrogen supplied. The solution concentrations followed the system of Nichols et al. (80) to demonstrate the effect of nitrogen source in a medium free of nitrifying microorganisms. Each solution contained 112 ppm N, 31 ppm P, 78 ppm K, 36 ppm Mg, and 160 ppm Ca. Cl and S varied, the Cl entering the ammonia solution as $Ca(Cl)_2$, and the ammonia solution also had a greater amount of sulfur from the ammonium sulfate. A 1/2 strength Hoaglands micronutrient solution and iron as Sequestrene 300 (0.5%), were added to each solution. The solution pH of each treatment and the mean leachate pH checked weekly, were as follows:

	NO_3	NH_4	Urea	NH_4NO_3
Solution pH	6.5	5.1	6.8	6.0
Leachate pH	7.9	5.4	6.9	6.9

Non-replicated tissue samples, using the first 6 fully mature leaves, were obtained just prior to the start and at the termination of the study.

The experiment was terminated on March 21, 1984, when over 50% of the plants of 2 treatments had died.

IV. RESULTS

Propagation

The portion of the stem used as propagative material significantly influenced the root dry weight and the percent rooting, but not the time required for the first appearance of roots for G. 'Ivanhoe' (Table 1). Root dry weight and rooting percentage were significantly greater when the softwood terminal was used as the propagative material and decreased for each section progressing down the stem. There was no significant difference in the time required for the first appearance of roots.

Table 1. Rooting response of selected two-node stem sections of G. 'Ivanhoe'

Section	Root Dryweight (mg)	Percent Rooting	First Appearance of Roots (days)
1	20.0 a[z]	77.7 a	36 a
2	9.0 ab	43.6 b	36 a
3	8.0 ab	22.7 c	36 a
4	6.0 b	16.2 c	36 a
5	4.0 b	8.0 c	36 a

[z]Means in the same column followed by the same letter are not significantly different at the 0.05 level using the Waller-Duncan K-Ration T Test.

The different stem sections used produced a significant difference in the percent rooting and the time required for the first appearance

of roots, but not in the root dry weight for G. 'Poorinda Peter' (Table 2). Best rooting, dry weight and percent was obtained for the 2-node softwood portion of the stem just below the terminal section while the terminal, semi-hardwood, and hardwood sections had lower root dry weights and rooting percentages. There was no significant difference in the time required for the first appearance of roots.

Table 2. Rooting response of selected two-node stem sections of G. 'Poorinda Peter'

Section	Root Dryweight (mg)	Percent Rooting	First Appearance of Roots (days)
1	2.0 a[z]	41.5 b	36 a
2	68.0 a	78.0 a	36 a
3	66.0 a	65.9 ab	36 a
4	65.0 a	56.6 ab	36 a

[z]Means in the same column followed by the same letter are not significantly different at the 0.05 level using the Waller-Duncan K-Ratio T Test.

Root dry weight, the percent rooting, and the number of days noted for the first appearance of roots was significantly affected by the portion of the stem used as the propagative material in G. x hookeriana (Table 3). The semi-hardwood and hardwood sections (sections 2, 3, and 4) had significantly higher dry root weights and percentages rooting when compared to the terminal section. The appearance of roots occurred six to ten days earlier for the terminal portion of the stem than in the three lower sections.

Table 3. Rooting response of selected two-node stem sections of G. x hookeriana

Section	Root Dryweight (mg)	Percent Rooting	First Appearance of Roots (days)
1	28.0 c[z]	62 b	29 b
2	63.0 b	88 a	36 a
3	103.0 a	92 a	36 a
4	82.0 ab	82 a	36 a

[z]Means in the same column followed by the same letter are not significantly different at the 0.05 level using the Waller-Duncan K-Ratio T Test.

Nutrition Studies

pH

G. glabrata. The range of pH levels significantly influenced all parameters used to measure its effect on this species (Table 4). The pH 4 plants were chlorotic, stunted, and root development was restricted when compared to the other pH levels. The dry weight of the roots and shoots, and extension growth was significantly less for the plants watered with the pH 4 solution compared to the other 4 pH levels. Although there was no significant difference in growth of plants grown at pH 5, 6, 7, and 8, the plants watered with the pH 8 solution were slightly larger.

Proteoid root development was completely absent in the plants watered with the pH 4 solution, and the number of proteoid roots,

although not significantly different, was higher in the plants watered with the pH 8 solution when compared to pH 5, 6, and 7 plants (Table 4).

Table 4. Effect of pH on growth and proteoid roots in Grevillea glabrata

pH	Dryweight		No. proteoid roots	Extension growth
	Roots	Shoots		
	(g)	(g)		(cm)
4	1.7 a[z]	3.5 a	0 a	2.5 a
5	5.4 b	12.4 b	5.8 b	21.1 b
6	5.8 b	12.0 b	6.3 b	24.3 b
7	5.8 b	12.9 b	5.8 b	24.5 b
8	7.3 b	14.0 b	9.3 b	27.9 b

[z]Means in the same column followed by the same letter are not significantly different at the 0.05 level using the Waller-Duncan K-Ratio T Test

The pH treatments produced some significant differences in the mineral composition of the leaves (Table 5). Plots derived from regression analysis performed on the mineral concentration of each element per gram dry leaf weight, were linear for N (r^2=.92), K (r^2=.85), Ca (r^2=.84), Zn (r^2=.09), Mn (r^2=.15), and Cu (r^2=.01), and quadratic for P (r^2=.33), Mg (r^2=.73) (Figures 1-3). In general, these plots show the highest levels of N, K, Ca, Mg, Zn, Mn, and Cu in the foliar tissue of pH 4 and steadily declined to pH 8. P content was highest in the foliar tissue at pH 6.

Table 5. Effect of pH on the foliar analysis of G. glabrata. (Mean % or ppm per gram dry foliage weight)

	pH				
	4	5	6	7	8
Element					
Percent					
N	2.47 a[z]	2.35 b	2.23 c	1.91 d	1.73 e
P	0.21 c	0.25 ab	0.26 a	0.23 bc	0.23 c
K	1.47 a	1.07 b	1.02 c	0.83 d	0.81 e
Ca	0.96 a	0.86 b	0.85 b	0.65 c	0.62 c
Mg	0.46 a	0.26 b	0.24 bc	0.21 c	0.23 bc
S	0.21 a	0.20 a	0.19 a	0.18 a	0.18 a
Cl	0.85 a	0.68 b	0.66 b	0.58 c	0.54 d
ppm					
Mn	23.9 a	12.9 bc	16.5 b	12.2 c	16.0 bc
Cu	34.3 a	37.1 a	34.0 a	34.2 a	32.0 a
Zn	34.3 ab	37.1 a	34.0 ab	34.2 ab	31.0 b

[z]Means in the same row followed by the same letter are not significantly different at the 0.05 level using the Waller-Duncan K-Ratio T Test.

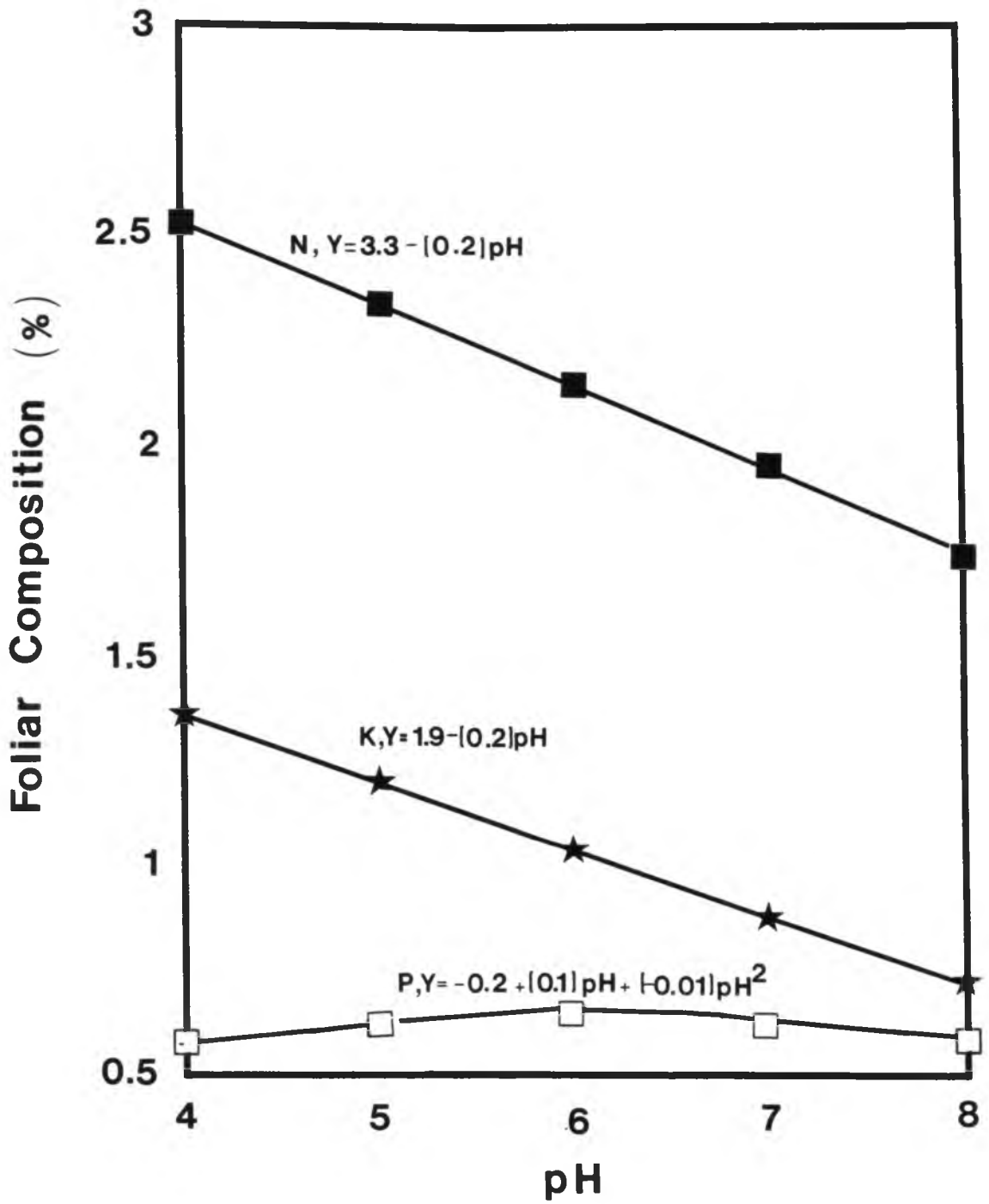

Figure 1. Effect of pH on the foliar tissue concentration of N, P, and K (%/gram dry foliar weight) in G. glabrata.

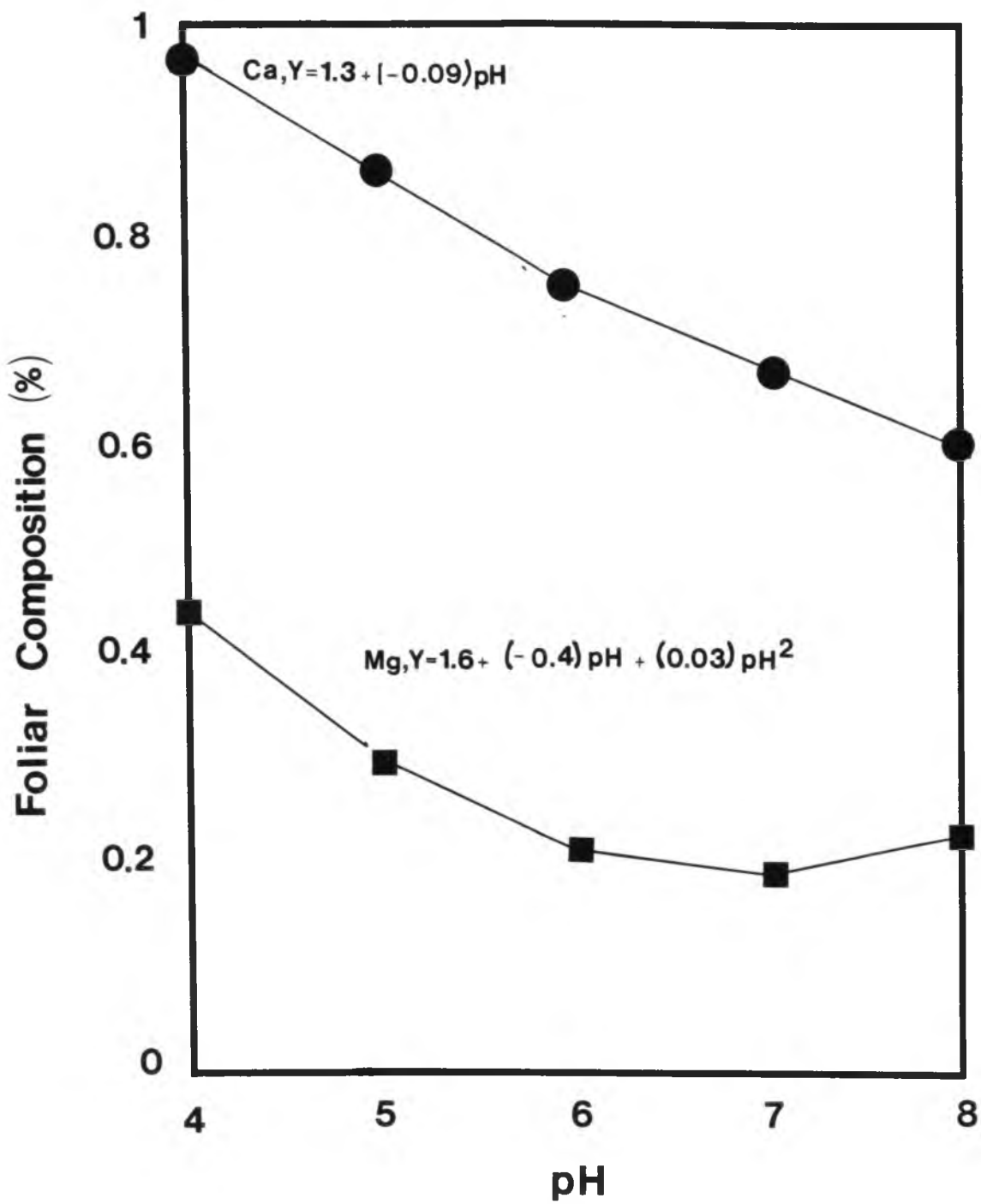

Figure 2. Effect of pH on the foliar tissue concentration of Ca and Mg (%/gram dry foliar weight) in G. glabrata.

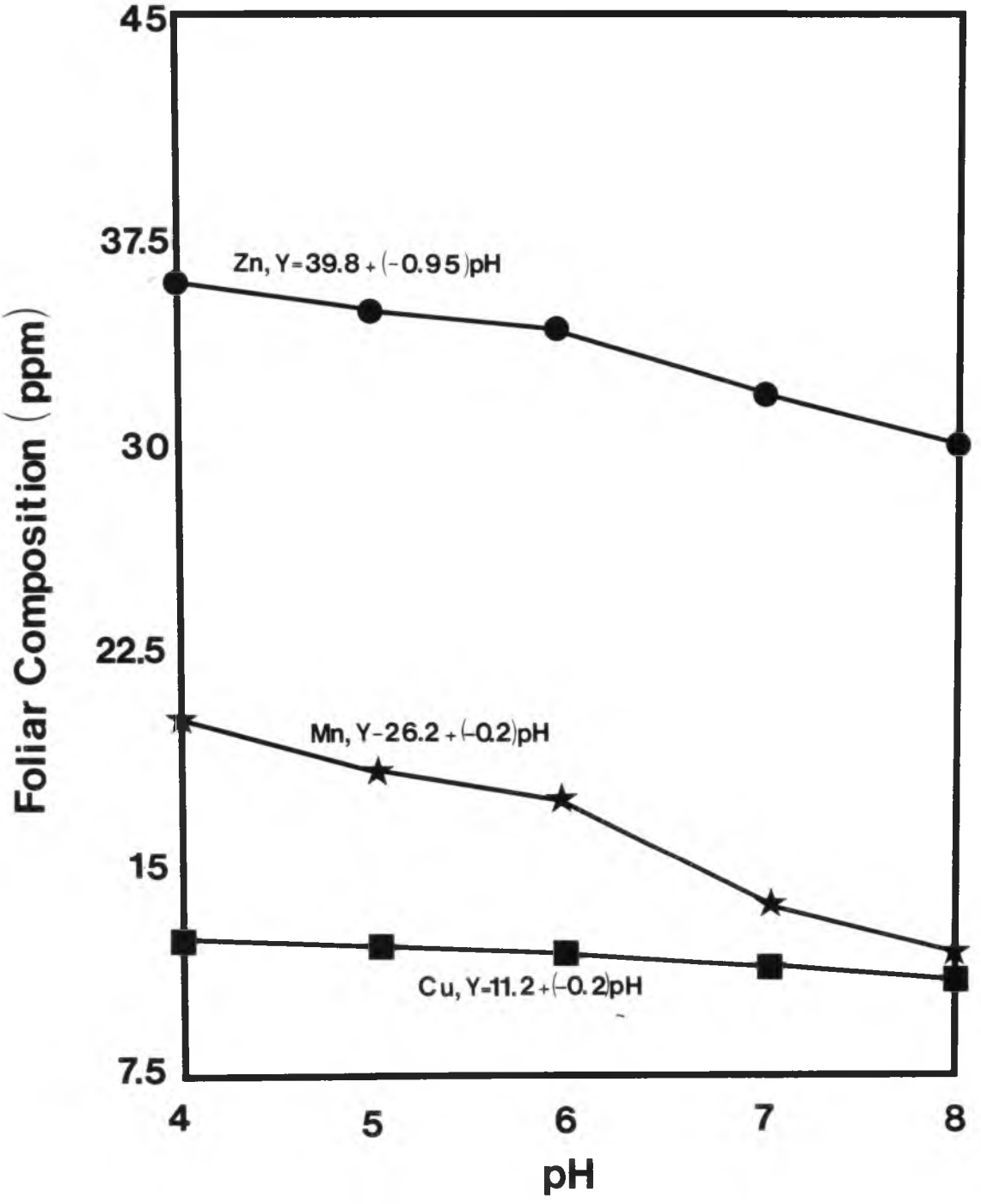

Figure 3. Effect of pH on the foliar tissue concentration of Zn, Mn, and Cu (ppm/gram dry foiliar weight) in G. glabrata.

G. biternata. The range of pH levels produced a clear trend in that for the parameters measured, the growth of the plants reached a maximum of pH 5 and 6 and declined at pH 4, 7, and 8 (Table 6). Dry weight of the roots and shoots were significantly greater in the plants watered with a pH 5 or 6 nutrient solution when compared to pH 8.

Extension growth of the shoots showed a significant increase at pH 5 and 6 when compared to pH 4, 7, and 8. The new growth increment of shoots of the pH 5 and 6 plants increased 2-3 times as much in length as those growing at the other pH levels.

Table 6. Effect of pH on the growth of G. biternata.

pH	Dry Weight		No. Proteoid Roots	Extension Growth
	Roots	Shoots		
	(g)	(g)		(cm)
4	0.4 ab[z]	2.1 ab	0	4.4 a
5	1.8 a	4.4 a	0	15.8 b
6	1.4 ab	4.4 a	0	12.0 b
7	0.6 ab	2.5 ab	0	4.9 a
8	0.2 b	1.2 b	0	4.1 a

[z]Means in the same column followed by the same letter are not significantly different at the 0.05 level using the Waller-Duncan K-Ratio T Test.

The absence of proteoid root development at any pH level indicates that this is not a result of the pH treatments but of the particular species. Not all Grevillea species have been observed to form these specialized roots (64, 65).

The foliar tissue analysis values showed significant differences between the treatments (Table 7). Regression analysis, which was performed on the mineral concentration per gram dry foliage weight, produced quadratic curves for all elements, some of which are plotted in Figures 4-6. All plots showed low levels of N, K, P, Ca, Mg, Cu, Zn; and a very high level of Mn at pH 4 and 8. In general, the plants grown at pH 6 contained the highest levels of all elements except Mn, which was the lowest at pH 6.

Table 7. Effect of pH on the foliar analysis of G. biternata. (Mean % or ppm per gram dry foliar weight)

	pH				
Element	4	5	6	7	8
Percent					
N	1.25 d	2.53 b	2.87 a	1.49 c	1.45 c
P	0.28 a	0.29 a	0.35 a	0.28 a	0.36 a
K	0.51 c	1.14 b	1.59 a	0.43 c	0.59 c
Ca	0.82 d	1.16 b	1.55 a	0.72 e	0.97 c
Mg	0.27 a	0.27 a	0.29 a	0.27 a	0.30 a
S	0.16 c	0.22 b	0.27 a	0.21 b	0.18 bc
Cl	1.36 b	0.76 d	1.12 c	1.56 a	1.26 b
ppm					
Mn	45.38 a	3.98 c	2.26 c	21.74 b	40.00 a
Cu	10 a	10 a	10 a	9 a	12 a
Zn	33.25 ab	36.50 ab	42.62 a	26.62 b	35.57 ab

[z]Means within the same row followed by the same letter are not significantly different at the 0.05 level using the Waller-Duncan K-Ratio T Test.

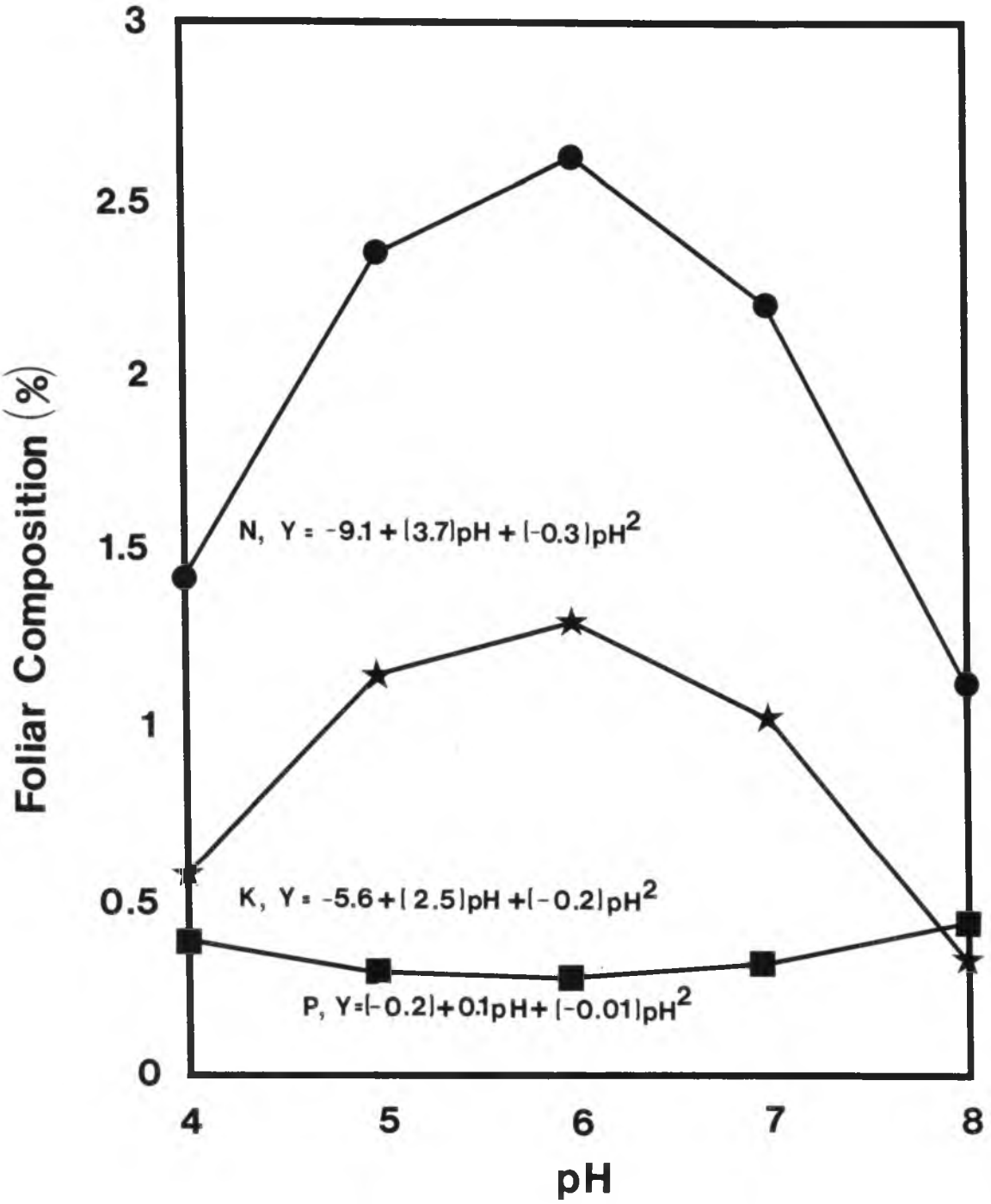

Figure 4. Effect of pH on the foliar tissue concentration of N, P, and K (%/gram dry foliar weight) in G. biternata.

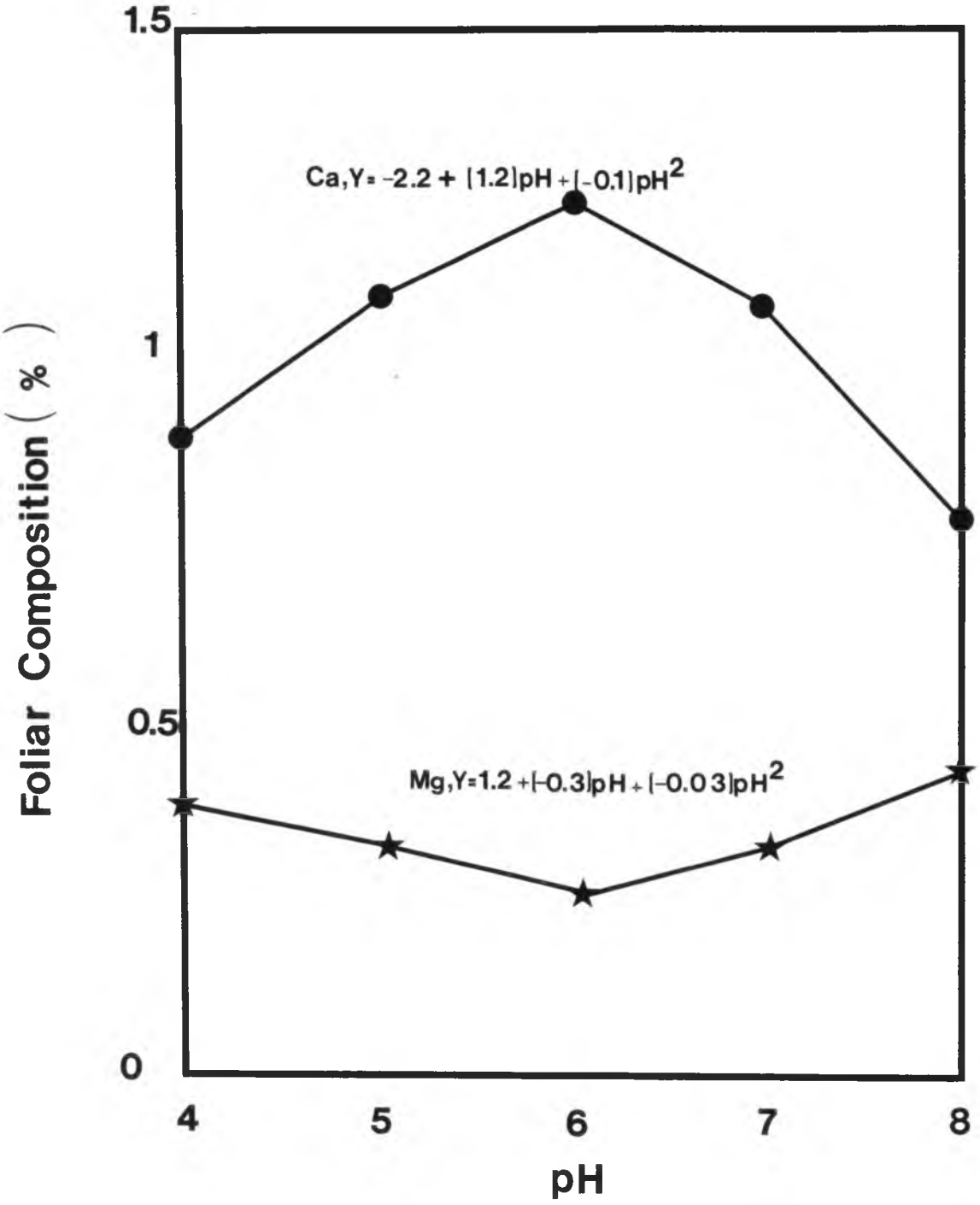

Figure 5. Effect of pH on the foliar tissue concentration of Ca and Mg (%/gram dry foliar weight) in G. biternata.

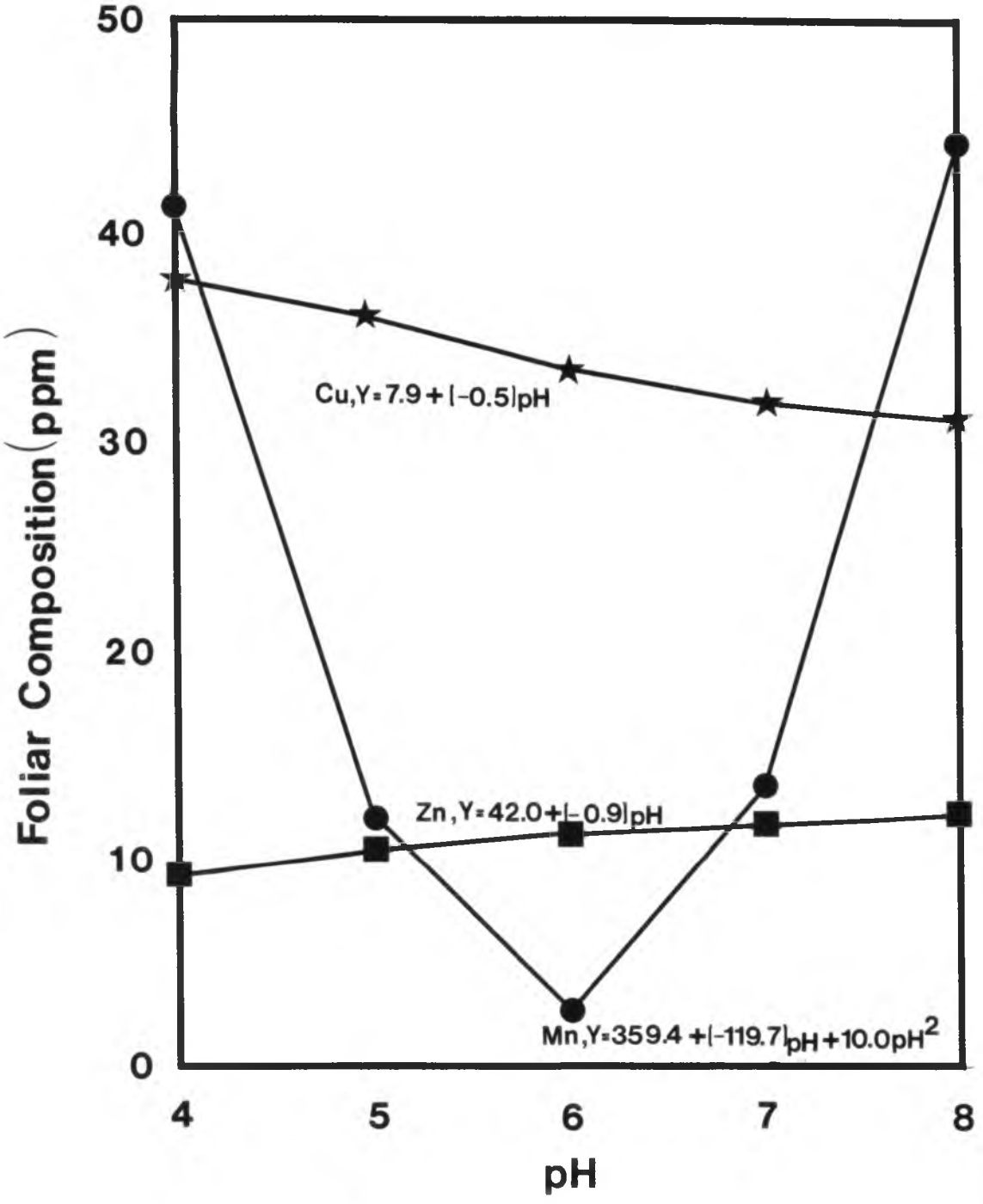

Figure 6. Effect of pH on the foliar tissue concentration of Zn, Mn, and Cu (ppm/gram dry foliar weight) in G. biternata.

Nitrogen-source

The dry weight of the roots and shoots were not significantly different in any of the four nitrogen-source treatments (Table 8). The plants supplied with NO_3-N and NH_4:NO_3-N had higher root dry weight, especially when compared to the NH_4-N treated plants and the shoot dry weight was lower in the ammonium-fed plants when compared to all other treatments.

Because of the intolerance of Grevillea to the levels of elements in the nutrient solution derived from Nichols (80), the plants in some treatments may not have been actively metabolizing the nutrients supplied, all growth ceased and extension growth could not be measured. However, 9 weeks into the study, plants watered with the NH_4-N and NH_4:NO_3-N nutrient solutions exhibited severe tip dieback. The following week, approximately 50% of the plants in both of these treatments began to lose leaf sheen, the foliage acquired a grayish tint, and within three days 70% of the plants in each treatment had died (Table 8). Visual examination showed the root tissue to be discolored and soft.

The experiment was terminated at this point (10 weeks) so tissue samples could still be taken before all plants from the ammonium and ammonium nitrate treatments had died. Statistical analysis could not be performed on the foliar analysis due to the death of a large number of plants in two treatments, but there appeared to be no major difference in the mineral content of the foliage that could explain the lethal effects of the NH_4-N and NH_4:NO_3-N treated plants (Table 9).

Table 8. Effect of nitrogen-source on the growth of G. rosmarinifolia after 10 weeks

N-source	Dry Weight		% Mortality
	Roots	Shoots	
	(g)	(g)	
NO_3-N	1.0 a[z]	2.4 a	0
NH_4-N	0.7 a	2.2 a	70
$CO(NH_2)_2$	0.9 a	2.4 a	0
$NH_4:NO_3$	1.0 a	2.8 a	70

[z]Means in the same column followed by the same letter are not significantly different at the 0.05 level using the Waller-Duncan K-Ratio T Test.

Table 9. Effect of nitrogen source on the foliar analysis of G. rosmarinifolia (Single sample data)

	No_3-N	NH_4-N	$CO(NH_2)_2$	$NH_4:NO_3$
Element				
Percent				
N	1.33	1.26	1.34	1.28
P	0.13	0.14	0.13	0.13
K	1.15	1.09	1.11	1.18
Ca	0.80	0.73	0.78	0.75
Mg	0.31	0.31	0.32	0.33
S	0.17	0.21	0.18	0.19
Cl	1.18	1.36	1.30	1.37
ppm				
Mn	80	47	75	77
Cu	31	102	45	49
Fe	124	148	153	140
Zn	43	41	45	41

V. DISCUSSION

Propagation

Research over many years has concluded that the structure and degree of differentiation vary from the tip to the basal portion of a stem (105). A number of workers have shown that when blueberry, sugar maple, and rose shoots are cut into segments, there is a gradient in rooting response from tip to base, depending on the nature of the material (24, 77, 105). The capacity to form roots in rhododendron almost completely disappears in stems with increasing shoot age and in asparagus, root initiation of excised shoot tips was decreased by increasing the length of the shoot tip cutting (86). The age of the tissue can significantly influence the amount of auxins, carbohydrates, and rooting cofactors that are produced and that accumulate.

The purpose of this study was to determine if there was a gradient in rooting response from the terminal position to the woody portion of a stem. The content of auxins, carbohydrates or rooting cofactors in the stem was not investigated in this study, but extensive research elsewhere has determined that the levels of all three factors may vary from the terminal portion of a shoot to its base and thus influence the rootability of each node along the length of a single shoot (18, 40, 41, 57, 59, 87, 99, 100, 101, 105). Structural barriers of the stem (10), inhibitors (2), along with environmental factors such as light (57, 36) and temperature (63), are also possible factors to consider when propagating a difficult-to-root plant.

The percent rooting differed according to the section of the stem used as propagative material in all three Grevillea hybrids. Root formation was limited or non-existent at certain nodes of the stem, which suggests that some root promoting factors, inhibitors, or structural barriers were present at some nodes and not at others. Apparently, in G. 'Ivanhoe', the tip section was the only portion of the stem which contained an optimum balance of necessary rooting factors, resulting in a higher rooting percentage and dry weight of the roots when compared to all other sections. The results obtained for G. x hookeriana were just the opposite, in that high rooting percentages and root dry weights resulted when any portion but the tip section was used as the propagative material. Although the root dry weights in G. 'Poorinda Peter' were not significantly different, use of the portion of the stem just below the tip (section 2) resulted in much higher rooting percentages when compared to the tip itself. Accordingly, to the results obtained in this study, it would seem advisable to keep cuttings from these three hybrids in morphological order from tip to base and use only those portions which result in the higher rooting percentages. The time required for the first appearance of roots may be considered a less important criterion to measure rooting since in the one hybrid in which there was a significant difference, that portion which rooted earlier also resulted in the lowest root dry weights and rooting percentage.

Nutritional Studies

pH

The work of Hoagland and Broyer (50) and Arnon et al. (5, 6) provided evidence that the selective absorption of ions and changes of the reaction in the culture solution were dependent not only on the gradient of H and OH of the root medium, but also on the metabolic activity of the roots. This activity is regulated by the oxygen, temperature, and the initial salt content, the form and concentration of the salts applied and the carbohydrate content, all of which determine the differential rate of ion accumulation. Most horticultural crops do well in a pH range of 6.0-7.0, although all of the nutrient elements are available in a much wider range (5, 6). In general, NO_3, K, PO_4, Mg, Ca, Mn, Cu, and Zn are available in a pH range of 4.5-7.5, but at the extremes of this range, competition between cations and H at low pH or between anions and OH at higher pH values can severely limit the uptake of each ion (90).

G. glabrata. It is well-documented in Australian literature that most of the Protaceae are sensitive to high levels of fertilization (95, 96, 97, 102, 103). The growth reductions observed at pH 4 appeared to be the result of a direct H^+ ion injury to the roots or to the increased foliar content of a number of the mineral constituents. When compared to the other pH levels, the plants grown at pH 4 contained the highest levels of most of the elements, but also resulted in severe growth reductions and a lack of proteoid roots. As the pH of the nutrient medium increased from pH 4 through pH 8, a linear decrease in the foliar levels of N, K, Ca, Mg, Zn, Cu, and Mn was

observed. The greater absorption of NO_3, PO_4, and Mn in acid soil solutions is well documented (5, 6, 50), while K, Mg, and Ca can be absorbed from a wider range of pH values (90). Proteoid roots, which are dense clusters of rootlets produced in many proteaceous species, have been found to be involved in the uptake of nutrients from low fertility soils (62, 64, 65, 67). They are not essential for nutrient uptake, since at moderate fertilizer levels they are usually not present and no growth reductions have been observed (103). The results of this study support the work of Lamont (64), who found in Hakea, also in the Proteacease ". . . that an increase in the pH of the soil is accompanied by a significant increase in the relative proteoid root production, and that an increase in the available K, Mg, NO_3, Ca, total N, and organic matter content is accompanied by a significant decrease in the number of proteoid roots to non-proteoid roots." The results of this study indicate that as the pH increased to pH 8, the number of proteoid roots increased, and it may be that in G. glabrata, as the pH was increased, the availability of the elements decreased. The greatest growth was obtained at pH 8 and these plants contained the lowest foliar mineral tissue levels. It therefore appears that the increased availability of many of the elements in nutrient solution culture at pH 4 may have been the cause of the observed growth reductions.

G. biternata. The results of this study suggest that this Grevillea species is sensitive to extremes in acidity or alkalinity, as evidenced by the severely decreased growth of all plants at pH 4, 7, and 8. Results of the foliar tissue analysis indicate that the

reduced growth was caused by the plant's inability to absorb most of the elements at these pH levels. The greatest dry weight of roots and shoots, extension growth and foliar levels of N, P, K, Ca, Mg, Zn, and Cu occurred in the pH range of 5.0-6.0. There was more Mn at pH 4, 7, and 8, which reflects the possibility of root damage at pH 4, 7, and 8, which may have contributed to the observed growth reductions. Injury to the roots in the pH 4, 7, and 8 plants could also have been caused by the lack of Ca and K, which other workers have found results in a loss of membrane integrity (5, 6, 90).

In summation, the range of pH levels which the two grevilleas were subjected produced large differences in the growth and mineral composition of the foliage, which partially supports the hypothesis that the pH of a growing medium was partially responsible for the results obtained in the field trials. The low pH of the soils at Nuuanu, Manoa, and Wahiawa may have been responsible for the low survival rates of G. glabrata when compared to the higher pH levels at Kualoa and Kula. Increasing levels of pH above 4 produced plants with greater dry weights, greater numbers of proteoid roots, and greater extension growth, but an optimum pH level was not found in this experiment, which suggests that this species has more pH tolerance at its upper (alkaline) range. Growth of plants at pH 4 was severely restricted when compared to the other pH levels, and this indicates a minimum near pH 5.0 for the growth of G. glabrata in sand culture.

For G. biternata, the results indicate that the pH range where optimum growth can be obtained is much narrower than for G. glabrata. A pH range of 5.0-6.0 would be optimal, and good growth outside of

this range may be difficult to obtain in sand culture. The results of the field trial study in relation to the growth of G. biternata in sand culture does not entirely support the hypothesis that the pH of the different locations was responsible for the survival rates at Kula (pH 6.3 ± .9), Nuunau (pH 5.2 ± .4) and Wahiawa (pH 5.2 ± .3), the plants grown at Manoa (pH 4.8-6.0) with a similar pH range did not survive. This difference in survival rates could have been due to the higher rainfall in Manoa in conjunction with less sunlight. The results of this study do support the field trial results that this species will not tolerate alkaline pH levels.

Nitrogen Source

Similar growth yields but very dissimilar rates of survival were associated with the different forms of nitrogen. It is possible that the presence of the ammonium ion was responsible for the high mortality rates in two of the treatments. All of the nutrient solutions contained the same concentrations of all elements, with the exception of the form of nitrogen applied and the presence of greater amounts of SO_4 in the ammonium solution. The concentration of elements derived from Nichols et al. (81) turned out to be too high and growth reductions resulted in all four treatments. Thomas (102) found that high levels of fertilization (>90 gN/m^3/month) in G. rosmarinifolia resulted in the same type of growth reductions observed in this study for all four treatments.

The visual symptoms observed just prior to the death of the ammonium- and ammonium nitrate-fed plants are in agreement with Thomas

(103), who found that high ammonium N (74gNH_4 -N/m^3 /month) caused severe growth reductions resulting in foliar dry weights which were less than those of a no-fertilization treatment. Pharis et al. (85) and Barker et al. (8) found that symptom development for ammonium toxicity was rapid in pine and bean, respectively. Within a few days of the initial symptom observance, the plants went from a normal green to gray and shortly thereafter died. The roots were shorter, stubbier and discolored, indicating that the ammonium ion itself may be responsible for the damage and not just a pH effect. The results of a study by Vines and Wedding (107) indicate that toxicity results from reactions of ammonia inside the cells, not just a pH effect of the growing medium. They suggested that at least part of the toxicity of ammonium is due to its ability to specifically inhibit the oxidation of DPNH and thus block the transport of electrons from oxidized substrates to oxygen in the mitochondria.

The pH drop usually associated with the reduced growth observed with a number of plants (15, 21, 22, 35, 61, 72, 88, 108) did not appear to be the cause of the high mortality rates in two of the treatments. The pH of the NH_4-N leachate was at 5.4, and that of the urea and ammonium nitrate leachates were 6.9. If pH drop of the root medium was solely responsible for the mortality rates in two treatments, then the NH_4NO_3 plants should not have died in the same numbers as the NH_4 plants, or a higher mortality rate should have been observed in the urea-fed plants.

In conclusion, in sand culture the form of nitrogen applied in this study produced results indicating that fertilization with

solutions containing ammonium as the sole or partial source of nitrogen was responsible for the high mortality rates in two treatments in G. rosmarinifolia. It seems reasonable to assume that under conditions of this study, nitrate or urea fertilization would be the "safest" forms of nitrogen to use with G. rosmarinifolia.

VI. SUMMARY

The portion of a shoot used as propagative material produced different rooting responses in all three Grevillea hybrids. For G. 'Ivanhoe', the stem section which includes the terminal gave significantly higher dry root weight and percent rooting when compared to all other segments of the stem. The terminal section of a shoot should be avoided as cutting material in G. 'Poorinda Peter', the results of the study showing much lower root dry weights and percent rooting for this section when compared to the lower sections. The portion just below the terminal gave the highest percent rooting and would seem the best propagative material. In G. x hookeriana, use of any section but the terminal resulted in higher root dry weights and percent rooting, and it would be advisable to avoid the terminal of a shoot as propagative material. In general, from the results obtained in the preliminary investigation, most grevilleas root easily as semi-hardwood of terminal cuttings when treated with a 2000 ppm IBA quick-dip solution. For the more difficult-to-root grevilleas, investigations such as this study may provide a grower with the information needed to propagate them. Air layerage, grafting, and tissue culture may provide alternatives in the propagation of some of the more difficult-to-root grevilleas.

The results of the pH study revealed a wide range of tolerance in G. glabrata, and the plants grew equally as well as long as the pH was near 5 or above. In sand culture, G. biternata exhibited a

much narrower tolerance to the range of pH levels studied, and this species may be confined to growing in the pH range of 5 and 6.

Different sources of nitrogen produced no significant differences in the dry weights of G. rosmarinifolia, but the sole or partial use of ammonium in this study was associated with high mortality rates in these two treatments. The nutrient levels adopted from another study were too high. Lower levels of fertilization may be better for these plants which are adapted to low fertility soils in their native Australian habitats.

VII. RECOMMENDED ADDITIONAL STUDIES

In each of the studies presented in this thesis, further research is necessary to clarify and perhaps expand the information obtained.

The results obtained in this study showed a gradient in rooting response from the terminal to the base of a shoot in G. 'Ivanhoe', G. 'Poorinda Peter', and G. x hookeriana. Physiological and biochemical studies are needed to determine if there are differences in the amounts of endogenous auxins, carbohydrates, rooting cofactors, or inhibitors along the length of a shoot. Morphological studies would possibly determine the presence or absence of structural barriers in the stem which may inhibit root formation.

The pH study was initiated from the results obtained in the 1981 field trials. The results reflected the possibility that pH was only partially responsible for the field trial results, and further studies on the effects of varying temperature, soil type, light and rainfall would be needed to clarify the field trial results.

Nitrogen sources containing solely or 50% ammonium resulted in high mortality rates in G. rosmarinifolia. Further studies using varying ratios of NH_4 to NO_3 would provide more information on the tolerance of this species to smaller amounts of the ammonium ion than that investigated in this study. The rates of fertilization used here were too high for all nitrogen source treatments as evidenced by the growth reductions in all four treatments, and further study is needed as to the nutrient levels and/or the frequency of nutrient solution applications in sand culture.

APPENDIX--SUPPLEMENTARY TABLES

Appendix Table A. Environmental characteristics of Australian locations where many *Grevillea* evolved (66, 112)

Location	Rainfall (cm/year)	Temperature (^{o}C)	Relative Humidity (%)	Drainage
Western Australia	40 - 100	winter: 7 - 18 summer: 13 - 32	winter: 60 - 70 summer: 40 - 60	well-drained seasonal swamps
Eastern Australia	50 - 130	winter: 7 - 18 summer: 16 - 32	winter: 60 - 65 summer: 60 - 70	well-drained some swamps

Location	Soil Characteristics	Nutrient Deficiencies	Soil pH
Western Australia	sand, lateritic gravel	N, P, K, Cu, Ca, Zn, Mo	alkaline to very acid
Eastern Australia	sand, gravel clay sub-soil	N, P, K, Cu, Ca, Zn, Mo	neutral to very acid

Appendix Table B. Environmental characteristics of five Grevillea plots in Hawaii (27, 106)

	Kualoa	Kula	Manoa	Nuuanu	Wahiawa
Elevation (m)	3.05	930.2	153	125	351
Rainfall (cm/yr)	106	102	412	280	152
Temperature (=C-ave/yr)	23-25	16-18	19-24	21-24	21-23
Temperature Extremes (ave/yr)	-----	10-28	13-30	-----	12-32
Sunlight	Full	Full	Semi	Full	Full
Soil pH	8.0 ± .1	6.3 ± .7	5.7 ± .9	5.2 ± .4	5.2 ± .3
Soil Salinity	.38	.28	---	---	---
Soil Characteristics	Layers of silty clay and sand	Loam: well-drained	Stoney clay loam well-drained	Silty clay loam, well-drained	Silty clay well-drained
Fertility					
P	very low, <11 kg/Ac.	Low, <27 kg/Ac	very low, trace	very low, <11 kg/Ac	very low, <11 kg/Ac
K	High, 2724 kg/Ac.	Moderate 82 kg/Ac	very low, 18 kg/Ac	very low, <18 kg/Ac	very low, 18 kg/Ac
Ca	High, 2724 kg/Ac	High, 2270 kg/Ac	very low trace	low, 227-681 kg/Ac	very low 227 kg/Ac
Mg	Mod.-high 1135 kg/Ac	Low-mod. 341 kg/Ac	very low <114 kg/Ac	Low-mod. 363 kg/Ac	very low 168 kg/Ac

Appendix Table C. Survival of *Grevillea* sp. at 5 sites in Hawaii

	Location				
	Kualoa	Kula	Manoa	Nuuanu	Wahiawa
site pH:	8.0 ± .1	6.3 ± .7	5.7 ± .9	5.2 ± .4	5.2 ± .3
Grevillea					
G. biternata	-	+	-	+	+
G. gaudichaudii	-	+	+	+	+
G. glabrata	+	+	-	-	-
G. australis v. *brevifolia*	-	-	-	-	=
G. bipinnatifida	-	+	-	-	+
G. 'Big Red'	-	+	-	-	-
G. 'Boongala Spinball'	-	+	+	+	+
G. brevicuspis	-	+	-	-	=
G. 'Canaberra Gem'	-	+	+	-	=
G. 'Canterbury Gold'	+	+	-	+	+
G. 'Clearview David'	-	+	-	-	+
G. x *hookeriana*	-	+	-	+	-
G. 'Molonglo'	+	+	-	+	=
G. 'Poorinda Beauty'	-	=	-	-	-
G. 'Poorinda Peter'	-	+	-	+	=
G. 'Rhondeau'	-	=	-	-	-
G. rosmarinifolia	-	+	+	-	=
G. 'White Wings'	-	+	-	+	+

+ = 50% or more of those planted survived one year.

- = 50% or more of those planted did not survive one year.

= = the plant was not planted at the locality.

Appendix Table D. Effects of Five Commerical Rooting Preparations on the Rooting of terminal and stem cuttings in 11 Grevillea species or hybrids propagated November 1981.

Treatment	# Roots	% Rooting (per avg Trt)
G. australis v. *brevifolia*		
Control	16 a[z]	72 a
Hormex 3	14 a	78 a
Hormex 8	15 a	72 a
Rootone	15 a	60 a
Dip 'N Grow	15 a	60 a
Woods Rooting Compound	16 a	72 a
G. bipinnatifida		
Control	19 ab	57 a
Hormex 3	23 a	69 a
Hormex 8	17 ab	48 a
Rootone	15 b	43 a
Dip 'N Grow	15 b	40 a
Woods Rooting Compound	17 ab	54 a
G. biternata		
Control	15 a	22 a
Hormex 3	21 a	42 a
Hormex 8	21 a	42 a
Rootone	17 a	29 a
Dip 'N Grow	27 a	66 a
Woods Rooting Compound	25 a	66 a
G. 'Boongala Spineball'		
Control	15 a	10 b
Hormex 3	19 a	40 ab
Hormex 8	20 a	37 ab
Rootone	24 a	60 a
Dip 'N Grow	19 a	47 ab
Woods Rooting Compound	23 a	48 ab

Appendix Table D (continued)

Treatment	# Roots	% Rooting
G. brevicuspis		
Control	21 b	58 a
Hormex 3	26 ab	75 a
Hormex 8	29 a	78 a
Rootone	29 a	78 a
Dip 'N Grow	30 a	80 a
Woods Rooting Compound	30 a	78 a
G. caleyi		
Control	5 ab	33 ab
Hormex 3	3 b	20 b
Hormex 8	6 a	40 ab
Rootone	6 a	40 ab
Dip 'N Grow	7 a	66 a
Woods Rooting Compound	5 ab	40 ab
G. x gaudichaudii		
Control	20 c	28 c
Hormex 3	30 ab	62 abc
Hormex 8	38 a	78 a
Rootone	30 ab	56 abc
Dip 'N Grow	22 bc	42 bc
Woods Rooting Compound	33 a	66 ab
G. glabrata		
Control	32 bc	100 a
Hormex 3	30 c	92 a
Hormex 8	31 bc	97 a
Rootone	32 b	97 a
Dip 'N Grow	35 a	97 a
Woods Rooting Compound	34 a	97 a
G. jephcottii		
Control	30 b	89 a
Hormex 3	31 ab	91 a
Hormex 8	33 ab	100 a
Rootone	33 ab	100 a
Dip 'N Grow	34 a	97 a
Woods Rooting Compound	33 a	97 a

Appendix Table D (continued)

Treatment	# Roots	% Rooting
G. 'Poorinda Peter'		
Control	14 a	23 b
Hormex 3	21 a	66 a
Hormex 8	19 a	53 ab
Rootone	17 a	50 ab
Dip 'N Grow	20 a	66 a
Woods Rooting Compound	18 a	50 ab
G. rosmarinifolia		
Control	43 c	96 a
Hormex 3	44 bc	100 a
Hormex 8	46 abc	98 a
Rootone	44 abc	96 a
Dip 'N Grow	48 a	100 a
Woods Rooting Compound	48 ab	98 a

[z]Within species or hybrids, means in the same column followed by the same letter are not significantly different at the 0.05 level using the Waller-Duncan K-Ratio T Test.

Appendix Table E. Horticultural Characteristics of selected Grevillea (16, 17, 31, 53, 99, 112)

Species/Hybrid	Growth Habit	Height	Leaf Shape	Flower Color/Form	Uses
G. asplenifolia	Erect shrub	12'-15'	Fern-like, toothed	Red, "toothbrush"	Specimen, rock gardens
G. biternata	Prostrate shrub	< 1'	Small, forked narrow	Masses of white fragrant fls.	Groundcover rockery plant
G. 'Boongala Spineball'	Spreading shrub	to 5'	Lanceolate, toothed	Red, "toothbrush"	Specimen
G. brevicuspis	Erect shrub	3'-4'	Small-toothed, prickly leaved	Fragrant, mauve to white clusters	Cut foliage
G. caleyi	Spreading or prostrate shrub	to 6'	Pinnate, with soft hairs	Red, "toothbrush"	Specimen, cut foliage/flowers
G. 'Canberra Gem'	Erect shrub	to 7'	Dark green, needle-like	Red, small	Specimen
G. gaudichaudii	Prostrate shrub	< 1'	Oat-shape, new leaves red	Red, "toothbrush"	Groundcover
G. glabrata	Erect shrub	to 9'	Gray-green, holly-like	Small, fine, white pendants	Hedge/screen, cut foliage
G. x hookeriana	Erect shrub	to 9'	Pinnate, narrow	Bright red, "toothbrush"	Hedge/screen, cut/foliage/ flowers
G. illicifolia	Spreading shrub	3'-4'	Holly-like, toothed	Dark red-purple, "toothbrush"	Specimen
G. 'Ivanhoe'	Erect shrub	to 12'	Gray-green, toothed, and lanceolate	Mauve, pendants	Cut foliage

Appendix Table E (continued)

Species/Hybrid	Growth Habit	Height	Leaf Shape	Flower Color/Form	Uses
G. jephcottii	Erect shrub	to 7'	Hairy, gray-green, somewhat needle-shaped	Greenish, terminal	Specimen
G. 'Poorinda Peter'	Spreading shrub	to 8'	Pinnate, toothed red, silver hairs on underside	"toothbrush"	Cut foliage
G. 'Poorinda Royal Mantle'	Prostrate	< 1'	Elongate, oak-shaped	red/black, "toothbrush"	Groundcover
G. 'Robyn Gordon'	Spreading shrub	3'-4'	Deeply pinate	Large, red, "toothbrush"	Specimen, potted shrub
G. rosmarini-folia	Erect shrub	5'-6'	Needle-like	Small, red, waxy clusters	Hedge/screen, rockeries

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